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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, UNDER THE DIRECTION OF E. L. MARK. — No. 122.

THE DEVELOPMENT AND FUNCTION OF REISSNER'S FIBRE, AND ITS CELLULAR CONNECTIONS. A PRELIMINARY PAPER.

By Porter Edward Sargent.

With Two Plates.

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In a recent number of the Anatomischer Anzeiger (Bd. XVII. pp. 33–44) I have described the occurrence of Reissner's fibre in the canalis centralis of vertebrates, and I there promised the early appearance of a paper on its development. My further researches on its development and cellular connections have led to the discovery of a highly specialized apparatus, of which the so-called fibre forms a part. The subject has developed much larger aspects than was anticipated, and the consequent delay in the publication of my complete results makes necessary a further preliminary paper.

As described in the previous paper, Reissner's fibre lies in the cerebro-spinal fluid; it extends through the whole length of the canalis centralis and the brain ventricles to the anterior portion of the optic lobes, where it passes into the brain tissues; it gives off throughout the posterior portion of its course fine branches, which enter the tissue of the spinal cord.

In the present paper I hope to show briefly that there is normally in the central nervous system of all vertebrates a highly specialized apparatus, the cells of which lie in the optic lobes and send their axons into the optic ventricle and the central canal to form the so-called Reissner's fibre. I have investigated the occurrence of this apparatus in upwards of one hundred species, representing all the principal classes and subclasses of vertebrates. The development has been studied in about twenty different species, and has been more or less completely worked out in representatives of all the chief groups of vertebrates. In this paper I shall describe the apparatus and its development in a few char-

acteristic forms, reserving the more detailed account of the investigations for a later and more extended article.

In *Amia*, at about the time of hatching, there is in the anterior portion of the roof of the third ventricle a differentiation of the neuroblasts. Some of them have already increased in size, have become more nearly spherical and take the stain more deeply than the surrounding cells (Figure 1). These enlarged cells are concentrated for the most part in the median plane at the anterior end of the tectum opticum near the posterior commissure. During the first stage of differentiation there are from twenty to thirty of these cells, but by the development of indifferent neuroblasts they increase rapidly in number, so that by the end of the fourth day after hatching there are from eighty to one hundred of them. During the first day the tectum is only one cell thick. Each cell has a large nucleus — whose diameter is somewhat more than one half that of the cell — with a single deeply staining nucleolus.

During the first and second days the axons develop from the cells as extremely fine processes, which always appear on the side of the cell nearest the ventricle, directly towards and into which they grow. Early in the third day adjacent axons, now projecting into the ventricle, come together in groups and coalesce at their tips (Figure 2), appearing as a single fibril in their further growth through the cerebro-spinal fluid. In later stages these fibrils coalesce with others similarly formed, and in their growth backwards through the fluid of the ventricles and canal form what has been known as Reissner's fibre (Pl. 2, Figure 8.) During larval development the fibrils which make up Reissner's fibre coalesce more and more, until by the eighth day there are only six or eight separate divisions of the fibre in the ventricle, and later these are still further reduced in number by further coalescence. The cells also give off dendrites, which run backward through the substance of the tectum.

In the later development of the tectum opticum these cells undergo an apparent migration, due to the development of intervening tissue, as a result of which their relative positions are considerably changed; the cells become more crowded together. During these changes in position the axis of the cell may rotate through an arc as great as 180°. It is an interesting fact that the eccentric nucleus always retains its position at the side of the cell opposite that from which the axon emerges.

At about the time of hatching one may find in the extreme posterior end of the canalis centralis (Figure 5) a number of small cells, three to four micra in diameter, lying in the lumen of the canal and ventriculus

terminalis. The surrounding walls of the canal are made up of a single layer of cells, actively dividing. Certain of these cells become separated from the walls and pushed into the lumen. Of these many atrophy and disintegrate. Some eight to twelve of them persist and continue to develop. These cells, at first spherical, become spindle-shaped, as they increase in size. These posterior canal cells (as I temporarily call them) give off peripherally a number of dendrites which penetrate the tissue of the cord (Figure 3). From the tapering anterior end of the cell is given off the axon (Figure 4), which runs cephalad through the lumen, eventually coalescing with the axon of similar cells (Figure 5) and then continuing its growth cephalad. About the third day this system of forward-growing axons meets the system of axons from the cells of the tectum growing backward and the two systems coalesce in a way not yet clearly made out, to complete what has been called Reissner's fibre. This fibre, then, is a nerve tract, composed of axons running in opposite directions, both cephalad and caudad. The development of this apparatus as outlined for Amia is typical of all vertebrates.

The condition of the apparatus in *Selachii* is especially interesting. In the skate Raja erinacea the cells are of great size (25 μ to 30 μ in diameter), being the most conspicuous elements in the brain. They are three hundred to four hundred in number, and lie in two bands, one on either side of the median plane, extending the whole length of the roof of the optic lobe (Pl. 2, Figure 9). At the anterior end these two bands meet, forming a large group of closely aggregated cells. The cells are multipolar, giving off several processes in addition to the large axon, which is 2 μ to 3 μ in diameter. As in Amia, the nucleus is eccentric, being always at the side of the cell opposite that from which the axon emerges. The number of the capillaries in the neighborhood of these cells, supplying them with blood, gives evidence as to the extent of the activity of the cells.

Although these cells are so conspicuous in the brain of the skate, they have attracted but little attention. They were first seen by Rohon in selachians and correspond in position to the "Dachkerne" which have been described for Amphibians and Reptiles, the function of which has not been established.

The axons pass dorsad and laterad from their cells, turning either cephalad or caudad, and form two great tracts of non-medullated fibres of large size, which extend through the whole tectum opticum lateral and dorsal to the cells. The fibres running caudad can easily be traced to the posterior end of the tectum, whence they pass into the cerebellum

and come into close proximity to the Purkinje cells. The fibre tract which runs forward may be traced to the anterior end of the tectum, where the fibres converge, apparently forming Reissner's fibre, which emerges from the tectum into the ventricle at this point. Where Reissner's fibre leaves the brain tissue, the membrane covering of the roof of the ventricle is continued in a cone-like projection surrounding the fibre (Figure 9). Still another process given off from these cells passes peripherad nearly to the outer surface of the tectum, where it comes directly in contact with the endings of the optic nerve fibres. These cells, whose axons form Reissner's fibre, are, then, in direct connection with the eye through the optic nerve, and in turn are connected with the Purkinje cells of the cerebellum, which are known to coördinate muscular movements. The posterior canal cells in the selachians are of relatively large size and about a dozen in number.

In the *Cyclostomata* this apparatus is in a more primitive condition. In Petromyzon marinus it begins to develop some time after hatching, and is not fully established until the second month of larval life. In larvæ thirty days after hatching the cells form a small but well-marked group lying in the roof of the rudimentary optic lobes in the median plane, and occupying the whole thickness of the tectum (Figure 7). The axons emerge directly into the optic ventricle and unite in groups to form Reissner's fibre. These axons may continue backward to the fourth ventricle in three or four separate divisions, but in later development these coalesce more and more. At this stage the posterior canal cells are already developed and are sending their axons cephalad through the canal, but they have not yet united with the axons of the tectal cells running caudad.

In the adult Petromyzon Reissner's fibre passes through the canalis centralis and the fourth ventricle, from which it enters the brain tissue of the basal portion of the cerebrum and passing through this emerges into the third ventricle. Here it breaks up into several trunks and continues forward to the anterior portion of the ventricle, where after further division it enters the tectum.

The passage of Reissner's fibre for a portion of its course through the nervous tissue in cyclostomes is especially interesting as throwing light on a little understood structure in Amphioxus. Of the dorsal colossal nerve cells in the anterior portion of the central nervous system of Amphioxus, the largest and most anterior, designated by Rohde as the "kolossale ganglien-zelle," is median and lies across the lumen of the canalis centralis. The cell is in direct connection with the pigment spot.

The axis cylinder runs caudad in the median plane just ventral to the floor of the canal. I venture the conjecture that this cell represents, in Amphioxus, the tectal cells of craniotes, and that its giant axis cylinder is homologous with Reissner's fibre. In the phylogeny of this apparatus the cyclostomes would then furnish the connecting link between Amphioxus and the gnathostomes.

A number of experiments have been performed to determine the functions of this apparatus. The best results have been obtained with dogfish (Squalus acanthias), and small sharks (Charcarias littoralis). In these animals Reissner's fibre is of such size (10 μ to 20 μ in diameter) that it is possible to remove portions of it from the brain ventricles or canal for microscopical examinations. The operation of breaking the fibre

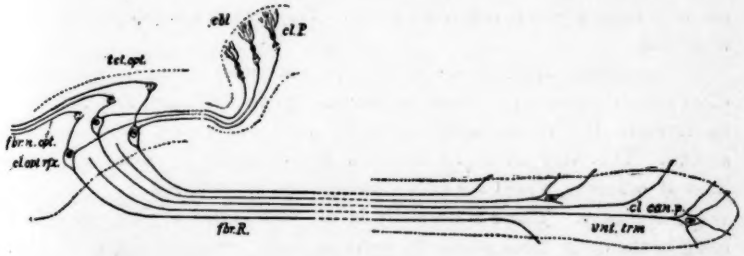

FIGURE A. Diagram of the optic reflex apparatus. *cbl.*, cerebellum; *cl. can. p.*, posterior canal cells; *cl. opt. rfx.*, optic reflex cells; *cl. P.*, Purkinje cells of cerebellum; *fbr. n. opt.*, afferent optic nerve fibres; *fbr. R.*, Reissner's fibre; *vnt. trm.*, ventriculus terminalis; *tct. opt.*, tectum opticum.

was easily performed. By an incision through the integument, and the removal of a small bit of cartilage, the tela choroideus covering the fourth ventricle was exposed. Through this a curved needle was plunged, and drawn several times transversely across the ventricle to break the fibre. The wound was then dressed; the animal, when replaced in the water, usually recovered from the shock in from twenty to thirty minutes. Those individuals in which the operation had been performed without success in breaking the fibre, served for the control experiments. The success or failure was ascertained at the autopsy, performed at death or on the fourth or fifth day after operation. Furthermore, the cord and medulla of each individual was preserved for microscopical examination. In about one third of the cases the operation had failed to

break the fibre. These individuals showed a marked difference in behavior from those in which the fibre had been broken. The former, after recovery from shock, were apparently normal in their reactions. Those in which the fibre had been broken showed a slowness in response to optical stimuli. For example, such an animal, in swimming about the tank in which it was confined, would bump into the sides of the cage. If any obstacle were suddenly placed in front of it while swimming, its effort to avoid the obstacle would come apparently too late to prevent collision. Those individuals in which subsequent autopsy and examination showed the fibre to be intact exhibited much greater dexterity and quickness in avoiding obstacles. The behavior of the animals operated on was constantly compared with normal individuals kept with them in the same enclosure. These experiments could be made entirely conclusive only by comparing the time reactions in cases where the fibre was cut with those where it remained uncut. No attempt has yet been made to do this.

The apparatus which is the subject of this paper forms, I believe, a short circuit between the visual organs and the musculature, and has for its function the transmission of motor reflexes arising from optical stimuli. This view as to its function is supported by many distinct lines of evidence, which are here classified and summarized.

(1) *Anatomy.* There is normally in all vertebrates a group of cells lying in the optic lobes which by some of their processes are in direct connection with the central terminations of the optic nerve, and by others with the Purkinje cells of the cerebellum. Their axons pass by the shortest route through the ventricles and canal to the posterior portion of the nervous system, where they pass into the cord and probably out through the ventral roots to the musculature. These anatomical connections make it probable that this apparatus is a direct path for the transmission of motor reflexes arising from optical stimuli. The connection with the Purkinje cells of the cerebellum, it is equally evident, is for the coördination of muscular movements.

(2) *Experimental Physiology.* When Reissner's fibre is cut or broken, the animal loses the power of responding quickly to optical stimuli. This is not due to the shock resulting from the operation, for animals on which the equivalent operation has been performed without breaking the fibre are nearly or quite normal in this respect.

(3) *Comparative Physiology.* (*a*) In any one group, as for example the teleosts, the apparatus has its highest development in those animals which are most active. In the predatory and rapacious bluefish (Poma-

tomus) the apparatus is highly developed, Reissner's fibre having a diameter of 10 μ. In Lophius, which is a much larger fish, but is usually sedentary and quiescent in its habits, and more dependent upon tactile than visual sensations for obtaining its food, the apparatus is degenerate and Reissner's fibre inconspicuous. (*b*) The corpora quadrigemina in higher vertebrates are degenerate organs, having given up most of their functions to other parts of the brain. In mammals they are, it is generally believed, concerned only with reflex functions. Assuming this to be true, the apparatus under discussion, since it has its centre in the corpora quadrigemina, must have, in the higher vertebrates at least, a purely reflex function.

(4) *Embryology.* (*a*) The apparatus does not reach full development until just before the animal attains free life. In the active fry of trout and salmon, which give reflex responses at this early age, it is fully developed at the time of hatching. In those forms in which the young are retained within the uterus of the mother until a late stage of development, as in mammals and some selachians, the apparatus is not developed until a relatively much later stage. (*b*) In sluggish larvæ the apparatus is not established until after the time of hatching; in Amia not until the fourth or fifth day, in Petromyzon not until the second month. This corresponds closely with the time at which these larvæ begin to respond promptly to definite optical stimuli from surrounding objects. (*c*) In those mammals which are born blind, as the mouse and kitten, the apparatus at birth is in a very incomplete state, so that it cannot be functional. In the mouse at birth the axons are just penetrating into the ventricle, and Reissner's fibre is as yet unformed.

(5) *Degeneration.* A study of the blind vertebrates of the cave fauna from the collections of Professor C. H. Eigenmann show that the optic reflex apparatus is reduced in direct proportion to the degeneracy of the eye. In those species which are totally blind no trace of this apparatus is to be found.

Experiments are now in progress to determine the effect of artificial extirpation of the eye on this apparatus.

Such a "short circuit" for the transmission of optical motor reflexes must be of great importance in saving time. If the impulse were transmitted from the termination of the optic nerve to the posterior musculature through the cord, it would involve transmission through a chain of from two to three neurons. Now, it is well known to psychologists that the time of transmission of a nerve impulse is delayed by passing through

a cell body, and by passing from one neuron to another. Wundt found that the delay in the spinal ganglion cell of man was 0.003 second. The delay in passing between different neurons is probably greater, say 0.005. So in man, if two cell bodies and two contacts between separate neurons are to be traversed, the loss of time would be ($[0.003 \times 2] + [0.005 \times 2] =$) 0.016 second. In lower animals, as is well known, the time reactions are much greater. It is quite probable that in some of the lower animals this short circuit may mean the saving of a considerable fraction of a second.

An animal suddenly confronted with some optical evidence of danger from which it recoils in fear, does so reflexly, calling into operation this apparatus. When we pause to consider how often in the struggle for existence the saving of a fraction of a second may be a question between life and death, we see how important a part this apparatus may have played throughout the vertebrate series in the survival of the fittest.

EXPLANATION OF PLATES.

Abbreviations.

cbl.,	Cerebellum.	*fbr. R.*,	Reissner's fibre.
cl. opt. rfx.,	Optic reflex cells.	*tct. opt.*,	Tectum opticum.
coms. p.,	Posterior commissure.	*vnt. III.*,	Third ventricle.
e'phy.,	Epiphysis.	*vnt. IV.*,	Fourth ventricle.

PLATE 1.

Figure 1. Amia calva, 1st day. Sagittal section (anterior end at right) through roof of mid-brain. The large cells in the tectum opticum are the tectal reflex cells, a few of which are just beginning to send out their axons.

Figure 2. Amia calva, 12th day. Sagittal section (anterior end at left) through anterior part of tectum opticum. The numerous fibrils entering the third ventricle are the axons of tectal reflex cells, a few of which are shown in the section, but the most of which are lateral to this section.

Figure 3. Amia calva, 6th day. Transverse section of the spinal cord through the ventriculus terminalis; posterior canal cell sending its dendrites through the fluid of the canal into the tissue of the cord.

Figure 4. Amia calva, 1st day. Sagittal section through the posterior end of the spinal cord and ventriculus terminalis, showing a single posterior canal cell, its long process directed cephalad.

Figure 5. Amia calva, 12th day. Sagittal section of a portion of the spinal cord near its posterior end; posterior canal cells in the ventriculus terminalis and canalis centralis, sending their axons forward to form Reissner's fibre. Reconstruction drawing from four successive sections.

Figure 6. Squalus acanthias, embryo 2 cm. long. Longitudinal sagittal section. Posterior canal cells in the canalis centralis sending dendrites into the cord and its axon cephalad.

Figure 7. Petromyzon marinus, 30 days. Sagittal sections of the tectum opticum (anterior end to the right); the axons of the developing tectal reflex cells are just emerging into the third ventricle.

PLATE 2.

Figure 8. Amia calva, 12th day. Sagittal section through brain, somewhat diagrammatic.

Figure 9. Raja erinacea, 14 cm. long. Sagittal section of the mid-brain, diagrammatic.

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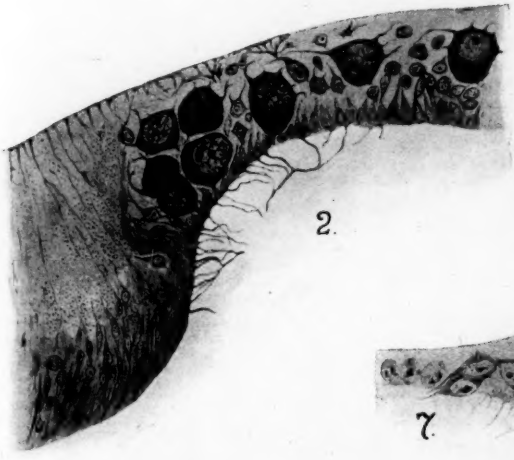

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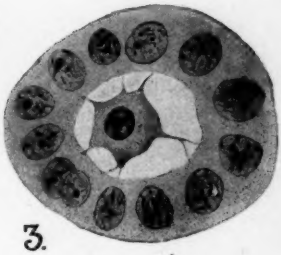

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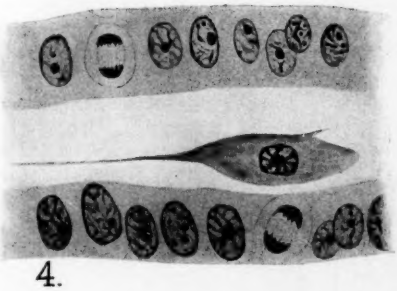

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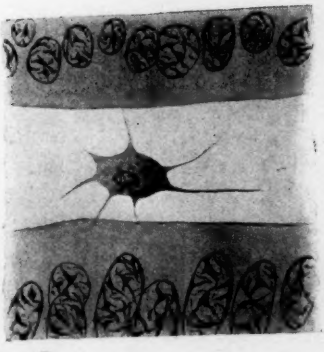

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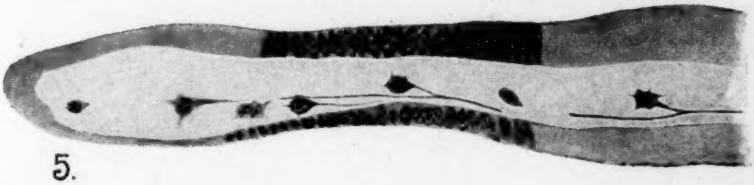

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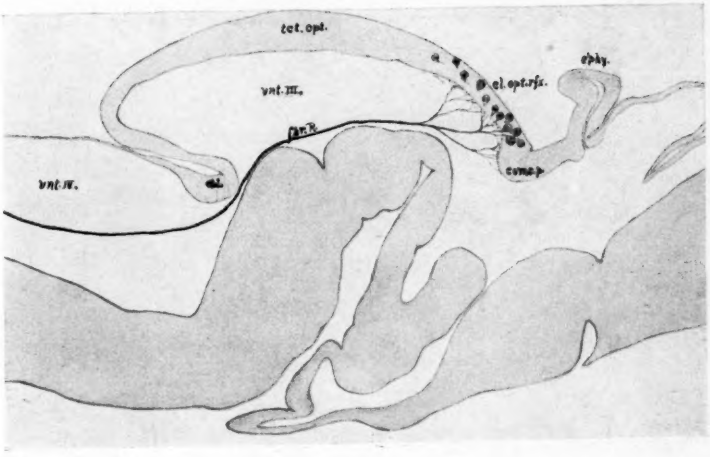
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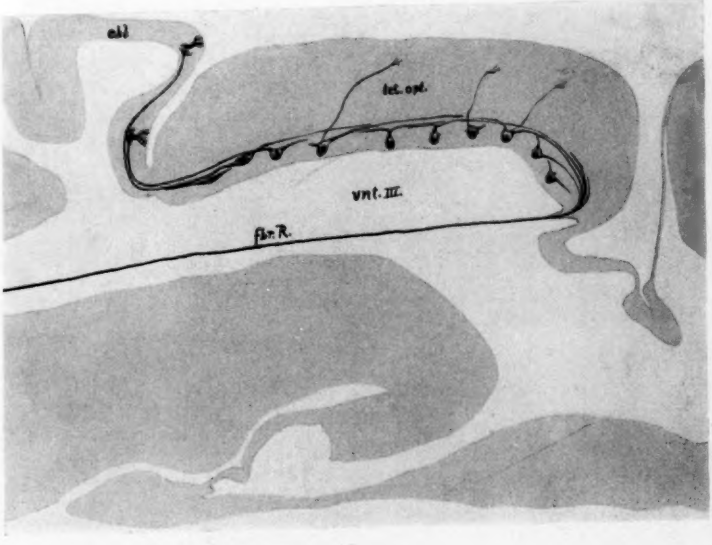
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